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THE ANATOMY OF AN EOLID, CHIORÆRA DALLI.

BY HAROLD HEATH.

In 1852 Gould[1] described a species of nudibranch, dredged in three fathoms of water at Fort Discovery, Puget Sound, establishing for it a new genus, *Chiorœra,* whose translated diagnosis is as follows: Body limaciform, head very large, pedunculate, semiglobose; oral face ventral, discoidal; mouth longitudinal, surrounded by a double series of cirri; cephalic tentacles foliate, retractile; branchial folds fan-shaped, arranged in a series on each side; genital opening removed from the almost dorsal anus." The species is further characterized by a pearly and whitish-colored body finely reticulated with orange. The cirri likewise are orange colored, and the cephalic tentacles are capable of retraction within a special sheath. The total length of the body is five and one-fourth inches.

On the 26th of July, 1913, I collected a number of specimens of what appear to be a new species of this genus in Rose Inlet on the eastern shore of Dall Island in southeastern Alaska. Two days later a few other individuals were taken in Hecate Strait near Hetta on the western coast of Prince of Wales Island. To Mr. W. F. Thompson I am indebted for additional material collected at Echo Harbor and Sewell Inlet on the eastern coast of the Queen Charlotte Islands.

The present species appears to be largely confined to the littoral zone, as the larger number of specimens were collected on algæ in shallow water. Nevertheless, a considerable number were found swimming near the surface, in some instances fully three hundred yards from shore. As they crawl about the great head is frequently contracted with considerable violence, possibly for the purpose of dislodging small organisms which serve as food. Sections of the alimentary canal, however, show it to be entirely empty, in all of the individuals critically examined, with the exception of one containing a few diatoms, so that we have little information indeed concerning the usual bill of fare. In the act of swimming the head is contracted as much as possible and the body is strongly flexed from side to side. Large numbers of eggs were found attached to "eel grass" and imbedded in gelatinous, spirally wound folds after the fashion of many nudibranchs.

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[1] U. S. Exploring Expedition, vol. 12, pp. 309–311.

The following are the measurements of the largest specimen: total length three inches, diameter of head one and one-half inches, greatest width of body one-half inch, greatest width of foot one-fourth inch, greatest height of body three-fourths inch. No pigment is visible in the skin of living animals, though the body wall has a milky appearance and is sufficiently transparent to show the light blue and reddish viscera within.

External Features.—The body (Pl. XI, fig. 1) comprises two distinct divisions, the head and body proper. The head presents the appearance of a low vault or cowl provided with two dorsal tentacles, two sets of marginal tentacles and on its under surface bears the mouth. Unlike *Chiorœra leonina,* the dorsal tentacles are not retractile, and in preserved material are plain, muscular, foliaceous outgrowths. Gould states that the tentacles of *C. leonina* bear on their anterior margins "an opaque, whitish papilla, presenting something of a spiral or lamellar structure." Nothing of the kind has been found to exist in the present species.

The marginal head tentacles form two series, an outer set comprising from fifty to seventy-five large, slender processes, and an inner fringe formed of much smaller outgrowths of approximately double the number. Each of these cirri is provided with a nerve (Pl. XI, fig. 2) and gives evidence of being a tactile organ, though observations along this line were very incomplete.

The mouth presents the appearance of a longitudinal slit (Pl. XI, fig. 1) placed near the posterior margin of the head, and therefore in close proximity to the anterior margin of the foot. Its posterior border may be said to be formed by the free border of the head, which here forms a deep angle usually devoid of the larger type of tentacle. Laterally and anteriorly the oral opening is surrounded by prominent, swollen lips. In living and in certain preserved specimens, the head region for some distance beyond the lips forms a prominent swollen area, occasionally thrown into temporary ridges. Sections show this area to be highly vascular. Unfortunately, more pressing duties made it impossible to make careful observations on living animals, and an exact description of the normal appearance of this area is now impossible. It may be added that in Gould's figure of *C. leonina* the mouth occupies a central position beneath the cephalic vault or cowl, whose tentaculate margin encompasses it at a considerable distance.

The body, separated from the head by a distinct cleft forming a neck, is roughly conical in form, and ventrally is traversed throughout its entire extent by a slender foot. Dorsally it carries a number of lappets in two longitudinal series attached along the junction of the dorsal and lateral surfaces of the body. All of the specimens in hand were preserved in formaldehyde, and while this served admirably to preserve the general appearance and proportion of parts, practically all of the lappets were found to be detached when the material was unpacked for study. It is certain, however, that each lappet is attached to the body by a slender stalk, and is leaf-like in form. The only doubtful point concerns their exact number. Judging by the slight circular scars where they were attached to the body, there appear to be five on the left side and four on the right, the place of the second largest one on the right being occupied by the anal opening. In a few large specimens there are traces of an additional, very small pair near the posterior end of the body. Each is penetrated by ramifications of the liver branches and by a system of blood sinuses.

The genital openings are on the right side of the body in the neck region, while the anal opening is far removed on the dorsal side of the animal.

Internal Anatomy.—In this species no distinct visceral cavity or spacious primary body cavity exists, the various systems of organs being surrounded by a loose meshwork of connective tissue and muscle fibers with the intercommunicating spaces serving as blood sinuses. Dissection accordingly is a comparatively simple matter, and the different systems of organs, especially the nervous, have been traced out in considerable detail. A description of each of these will now be given.

Considering first the digestive system, we find that the posterior border of the snout is deeply cleft along the midline, and, lacking the larger tentacles at this point, forms the ventral border of the mouth opening. The remaining margin is fashioned into thick, swollen, glandular lips united anteriorly, and of such length that the mouth appears as a longitudinal slit three or four millimeters in length.

The esophagus or pharynx (Pl. XI, fig. 4) is a comparatively short tube, and owing to the ventral position of the mouth the dorsal wall is considerably longer than the ventral. Immediately beyond the mouth opening the walls are relatively thick and without folds, but as the brain region is approached the inner lining becomes thinner and is thrown into numerous longitudinal folds. Probably not less than a dozen digestive tracts were either sectioned or opened carefully, but in no instance was there a trace of jaws, radula or distinct salivary glands.

Posterior to the central nervous system the lining of the pharynx becomes smoothed out before uniting with the smooth-walled stomach. Externally there are no noteworthy features to be noted in this section of the gut. It may be said, however, that the stomach is somewhat shorter than the pharynx and of considerably greater diameter. On the left side of the stomach are two sac-like dilations and one on the left, all of which are in communication with ducts from the digestive gland. In sections the lining epithelium of each of these sacs is seen to be thrown into a few high folds that are more or less continuous with lower longitudinal ridges extending throughout the main hepato-pancreatic duct.

As noted previously, the ventral gastric surface is longer in an antero-posterior direction than the dorsal, and the intestine is thus inclined dorsally, forming a distinct dorsal cleft between the stomach and intestine. Beyond this point the gut proceeds posteriorly, sinking slightly toward the ventral surface of the body, and also curving to the right until it reaches a point on the right side of the animal near the middle of the body. Here it curves dorsally, and expanding considerably opens to the surface. The intestinal epithelium is fashioned into several folds, visible externally through the thin wall, of which one, the dorsal, is highly developed and continues like a typhlosole throughout the entire length of the gut.

In preserved material the yellowish digestive gland is seen through the translucent body wall in the form of a dense mat generally distributed throughout the body, penetrating the lappets and extending into the snout as far forward as the tentacles. As can be seen in the figures, the follicles are united by an extensive system of ducts, which finally communicate with the stomach by means of one of the three openings noted previously.

The circulatory system can be disposed of in a few words, as the sinuses are unusually delicate and difficult to follow. The pericardium (Pl. XIII, fig. 13), situated anterior to the rectum, is a spacious thin-walled sac, with the ventral and posterior surfaces largely concealed by a mass of excretory tubules. The heart comprises an auricle and ventricle with their longitudinal axes directed in a dorso-ventral direction. The aorta, leaving the dorsal margin of the pericardial cavity, extends forward and soon disappears. On the other hand, the sinuses entering the auricle have been traced into the kidney and to a much less degree into the reproductive system and liver.

The kidney (Pl. XIII, fig. 13) lies on the dorsal side of the body, immediately above the anterior half of the hermaphroditic gland. In two specimens it was relatively thin and sheetlike, while in half a dozen other cases it occupied practically all of the space between the ovotestis and the body wall. As may be seen in fig. 13, the most conspicuous feature of the excretory system is a long and slender, thin-walled reservoir, somewhat crescent-shaped in lateral view. The form, however, is more or less irregular, owing to great numbers of diverticula springing from its surface. Each diverticulum divides several times, the number of divisions corresponding roughly to its diameter, until it finally breaks up into a number of thin-walled, transparent, blind-ended tubes comprising the major portion of the kidney.

From the central and most elevated portion of the main reservoir a wide cylindrical duct arises, which, narrowing as it pursues a course dorsally, opens upon the surface of the body on the left side of the anal opening. For a portion of the distance this canal is in contact with the rectum, and the excretory and anal openings are accordingly very close together. As indicated by the drawing (fig. 13), the ureter bears several excretory diverticula, and becomes muscular and non-glandular only in the neighborhood of the external opening. The reno-pericardial canal likewise is borne on the dorsally directed ureter in the form of a short, inconspicuous tube, terminating in much folded, ciliated nephrostome.

The reproductive system forms a conspicuous and compact mass in the posterior half of the body (Pl. XII, figs. 6, 8, 9). Of the various component elements, the gonad, occupying the posterior half of the visceral cavity, is the largest and presents the appearance of a slender conical organ comprising vast numbers of lobules. In section each of these is seen to be composed of several short acini communicating near the excurrent duct with a common chamber. Spermatozoa are developed in the more central acini, while those more externally placed contain ova only.

From each lobule of the gonad a slender duct arises, unites with a corresponding duct from some other lobule, and these unite with other and larger tubes, until finally the resulting main duct, the hermaphroditic canal, is formed that courses along the entire ventral face of the gonad. At the anterior border of the gonad it expands perceptibly, and in the form of a yellowish, smooth-walled structure undergoes a few twists, and upon decreasing its diameter divides into two branches, the oviduct and vas deferens, respectively.

The oviduct (Ov), the more dorsal of the two branches, comprises three main divisions, of which the first is relatively the most slender and forms a highly convoluted mass at the anterior end of the gonad at a somewhat higher level than the remaining elements of the accessory reproductive apparatus. This first section passes abruptly into the second, which is characterized by a greater diameter, much more highly developed muscular walls, and a more open arrangement of the coils. Near its union with the third division, comprising the albumen and mucous glands, it communicates with a slender seminal receptacle (Sr), empty in all of the dozen specimens examined. The mucous gland (Mu) is considerably larger than the albumen, with relatively smooth, thin walls thrown into gentle folds internally. The albumen gland (Al), on the other hand, is externally folded to a conspicuous degree, especially in its distal half. It communicates at its base with the mucous gland, and the secretory products from both make their way by a common canal which unites with the main section of the oviduct close to the external reproductive opening.

The vas deferens (Vd) enters almost immediately a compact gland, possibly functioning as a prostate, by means of several slender ducts which communicate in turn with numerous blind, finger-shaped hollow processes (Pa). Sections show these follicles to be composed of large, highly glandular cells, from many of which the secretion is in the act of escaping in the form of a finely granular colorless product. In some instances the hermaphroditic duct and the adjacent section of the vas deferens contain multitudes of spermatozoa; none occur in the supposed prostate. Beyond the prostate gland the vas deferens proceeds as a uniformly slender, much convoluted tube located immediately in front of the prostate. Distally it opens into the penis, a thick-walled, twisted structure communicating with the exterior by means of a pore immediately anterior to that of the female reproductive opening. A retractor muscle attaches to the base of the penis, and extending posteriorly divides, each half becoming inserted in the body wall about opposite the lateral border of the foot.

The central nervous system, presenting the highly compact appearance of the æolids in general, rests upon the dorsal surface of the esophagus or pharynx a short distance in front of the anterior border of the stomach. The cerebral ganglia are in close contact along the mid line, and posteriorly are closely united with the pleural ganglia. The lateral portions of the cerebral moiety are prolonged into short horns. On each side of the mid line a short connective leads from the posterior border of the cerebral ganglion and unites with a corresponding tentacular ganglion. Each of these last-named bodies is relatively small and rests in a depression between the cerebral ganglia, and in every specimen carefully examined the left is grooved and is considerably larger than the right. The pleural ganglia are more or less spherical bodies separated by a shallow depression from the cerebral and by a much deeper constriction from the pedal, which are therefore more clearly defined. The cerebral ganglia give rise to two or three pairs of nerves whose lettering in the following paragraphs is the same as in the figures.

C1, a nerve to the snout. In some instances this nerve has an independent origin; in other cases (as in Pl. XI, fig. 2, on the right side) it arises as a branch of C2. In any event, it soon divides repeatedly, and, so far as traced, forms a plexus, with ganglia at the nodes, that extends over the base of the snout in the middle area.

C2 is a heavy nerve extending through the loose tissue of the snout in the direction of the tentacle. About the middle of its length it divides, each half with its branches passing to the inside or the outside of the tentacle. The inner branch, after developing a few fibers, supplying the more median portion of the head, extends forward to the margin of the cowl. The outer branch, after dividing once or twice, likewise pursues a course to the margin. At the border of the cowl all of these nerves unite with an irregular nerve lying at the base of and supplying both sets of marginal tentacles.

C3 extends from each cerebral ganglion into the lateral portions of the cowl. After branching three times the resultant nerves unite with the marginal nerve. A short distance beyond its point of origin a connective unites C3 with C2.

Cx, a nerve springing from the ventral surface of each cerebral ganglion close to the cerebro-buccal connective (Pl. XIII, fig. 10). Extending anteriorly and ventrally, it enters the inferior wall of the esophagus. There are indications that it anastomoses with some of the nerves developed from the anterior surface of the buccal ganglion, but this has not been conclusively established.

C4, the tentacular nerve, which pursues a direct course from each tentacular ganglion into the tentacle, where it rapidly disappears from view among the dense mass of muscle fibers.

Each otocyst rests upon the dorsal surface of the central nervous system at the junction of the cerebral and pedal ganglion. In preserved material in surface view it appears as a yellowish, spherical body resting in a shallow cup of black pigmented cells. No sections of it were made.

Two pairs of nerves, in addition to the two commissures (Pc), arise from the pedal ganglia. The first of these is—

P1, a fairly heavy bundle springing from the side of the ganglion. Coursing through the dense mat of muscle and connective tissue composing the body wall, it extends posteriorly and ventrally, and divides at the junction of the body and head (Pl. XIII, fig. 11). The anterior branch supplies the body wall adjacent to the head, and sends a ventrally directed division to join the extensive plexus located in the foot. The posterior branch is distributed over the antero-lateral body wall, and in some instances also appears to be connected with the pedal plexus, though this has not been established with complete certainty.

P2 is a nerve likewise originating from the lateral surface of the pedal ganglion, but posterior to the foregoing nerve. Extending laterally and posteriorly, it divides opposite to the stomach into an anterior and posterior branch. The anterior division supplies the body wall posterior to the area adjacent to the external reproductive opening, and, extending to the foot, unites with the pedal plexus. The posterior branch continues posteriorly to a point about opposite to the level of the vas deferens, where it divides. The ventral division pursues a fairly direct course to the foot, where it unites with the pedal plexus. The dorsal branch continues its way along the side of the body to the posterior end of the animal. Throughout its course it develops at least four connectives which unite with the pedal plexus. Approximately one-third of its length beyond the point of origin, P2 gives rise to two dorsally directed branches. The anterior one passes forward and appears to anastomose with nerves from offshoots of x and y (fig. 12) arising from the pleural ganglion. The posterior branch, a slender nerve, pursues a course posteriorly and dorsally, and more or less parallel with P2 extends to the hinder end of the body. Throughout its extent it develops four branches, which pass into the dorsal lappets and about the anal opening, since this normally replaces one of the lappets on the right side.

The pedal ganglia are united by two commissures (Pc), the heavier one being anterior.

Four pairs of nerves usually pass out from the pleural ganglia. In certain cases this may become obscured on one or both sides through fusion or the presence of heavy connectives. In addition to these paired nerves, a single one—

G, appears on the right side (Pl. XIII, figs. 11, 12), emerging at a point close to the union of the pedal and pleural ganglia. Coursing ventrally and posteriorly, it finally reaches the region of the accessory reproductive apparatus, where it breaks up into several distinct branches. One of these disappears from view among the coils of the vas deferens, two or three minute twigs enter the penis, and in two specimens nerves have been traced into the seminal receptacle and into the oviduct adjacent to its external opening.

Pl1 arises from the antero-ventral border of the pleural ganglion. In one case it was represented by two nerves, but whether single or paired, it directs its course dorsally, and branching repeatedly is distributed to the dorsal body wall in the neck region.

Pl2, a somewhat stronger nerve than Pl1, near which it originates, extends in a postero-dorsal direction and after giving off one or two small nerves enters the most anterior and largest lappet.

Pl3 arises close to Pl2, at times fused with it basally, and likewise courses dorsally and posteriorly as far backward as the anal opening. Throughout its extent it gives off branches to the first lappet, which is also innervated by a branch from Pl2, and also to the second and third lappets. As the third lappet has no counterpart on the right side of the body, the corresponding nerve is distributed to the region about the anus. Attention has been called to the fact that the third lappet and anal region are likewise innervated by branches of P2.

Pl4 courses ventrally and after dividing becomes lost in the connective tissue and muscle fibers of the body wall close to the anterior margin of the foot.

Buccal System.—From the postero-ventral face of the cerebral ganglia the cerebro-buccal connectives arise, and coursing around the sides of the pharynx or esophagus unite with the buccal ganglia (Pl. XIII, fig. 10, B) at the sides of the digestive tract. The buccal ganglia are more or less globular bodies, and in addition to the cerebro-buccal connectives each is attached to three other nerves, of which one is the commissure extending beneath the pharynx to join its fellow of the opposite side. Of the remaining two nerves one is comparatively short, and extending anteriorly unites almost immediately with a nerve originating more dorsally from the cerebro-buccal connective. Beyond this point of union the combined bundle extends anteriorly and ventrally, and after forming a plexus becomes lost among the muscles of the pharynx. The last buccal nerve to be considered pursues a posteriorly directed course from the buccal ganglion, and very soon unites with the smaller of the two pedal commissures. Posterior to this point it continues along the sides of the pharynx to a point about midway between the level of the central nervous system and the first liver pouch. Here it divides, one branch extending dorsally to enter the pleural ganglion or the base of Pl3, while the ventral branch is directed to the ventral wall of the pharynx where it breaks up into several branches. Both of these last-named nerves give rise to a single offshoot, each of which continues backward to the anterior border of the first liver pouch where they enter a strong, ganglionated commissure, passing over the dorsal wall of the pharynx. The lower of the two nerves just mentioned develops a nerve, before entering the dorsal commissure, which is directed posteriorly beneath the first liver pouch and branches over the ventral wall of the stomach. Another nerve, having a similar course, arises from the ganglion, and curving around the ventral margin of the pouch becomes lost on its walls after branching two or three times.

As noted previously, the dorsal buccal commissure is ganglionated at the point of union with the two nerves connected more anteriorly with the buccal ganglion, and posteriorly this ganglionated section extends along the sides of the stomach to the posterior border of the first liver pouch. From it a clearly defined nerve arises, and extending dorsally follows the bile duct into the liver proper, where it breaks up and can be seen extending along some of the larger follicles. At the posterior end of the liver pouch the buccal nerve divides, the ventral branch supplying the liver pouch and the ventral wall of the stomach. The dorsal branch extends posteriorly along the sides of the stomach, and upon reaching the second liver pouch forms several branches, all but one of which enter the liver pouch. The exception is a distinct nerve (Bi) which continues along the sides of the intestine, where it soon forms with its fellow a plexus that has been followed to the anal opening. There are indications that in the anal region this plexus becomes continuous with branches from Pl3 or P2, which, as noted previously, are distributed to the body wall about the anus.

From the foregoing paragraphs it will be seen that the head, tentacles and otocysts are innervated solely by nerves from the cerebral ganglia. The neck region is supplied with branches (Pl1, Pl4) from the pleural ganglia. The entire ventral half of the body proper and the posterior dorsal half is provided with nerves (P1, P2) from the pedal ganglia. The remaining dorsal half is furnished with offshoots from pleural ganglion nerves (Pl2, Pl3). The ventral surface of the esophagus is innervated by nerves (Cx) from the ventral face of the cerebral ganglia. The stomach is supplied with at least three pairs of nerves having their origin in the buccal system. The liver pouches and gland itself likewise derive their nerve supply from the buccal nerve complex. From the same source a nerve on each side of the intestine forms a plexus throughout the length of the gut, and may connect with branches (P2c) from the pedal ganglia or with others (Pl3) from the pleural. The reproductive apparatus is abundantly supplied with branches of the nerve G having its origin in the right pleural ganglion. In two specimens there were faint indications that delicate twigs from this same source enter the heart and renal organ, but this was not definitely determined.

A brief diagnosis of the present species is herewith appended.

Genus **CHIORÆRA** Gould.

A description of the genus is given in the opening paragraph of the present paper. Type of the genus *C. leonina.*

Chioræra dalli new species.

Body limaciform, smooth and of a pearly color without definite signs of pigmentation. Head enormously developed, with the mouth near the posterior margin. Dorsal tentacles simple leaf-like expansions without special sheath. Jaws, radula and salivary glands wanting. Total length three inches. Off the coast of British Columbia, in shallow water.

It is with great pleasure that I associate the name of this species with that of the renowned student of west-coast conchology, Dr. W. H. Dall.

ABBREVIATIONS USED IN FIGURES.

Al	albumen gland.
B	buccal ganglion.
Bi	intestinal nerve.
C	cerebral ganglion.
C1, C2, C3, C4	cerebral nerves.
Cx	cerebro-esophageal nerve.
G	visceral nerve.
Lp	liver pouch.
Mu	mucous gland.
Ot	ovotestis.
Ov	oviduct.
P	pedal ganglion.
P1, P2, P3, P4	pedal nerves.
Pa	prostate gland.
Pc	pedal commissures.
Pe	pericardium.
P	pleural ganglion.
Pl1, Pl2, Pl3, P 4	pleural nerves.
Sr	seminal receptacle.
Vd	vas deferens.

EXPLANATION OF PLATES XI, XII, AND XIII.

PLATE XI.—Fig. 1.—*Chiorœra dalli,* ventral view.

Fig. 2.—Dorsal view of head, showing its innervation.

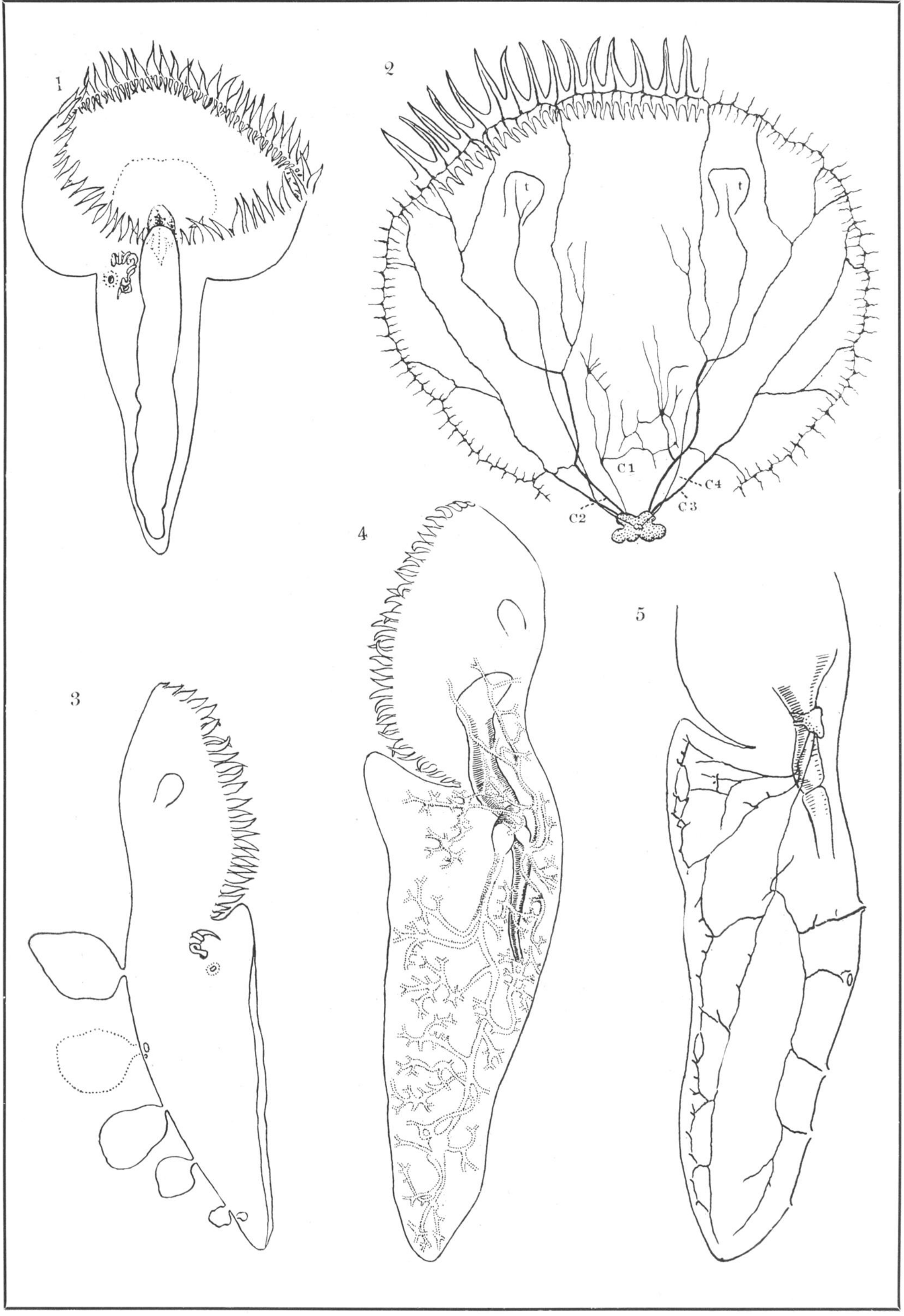
Fig. 3.—Side view of entire animal. Anal opening, near which is excretory pore, replaces lappet; left one shown in stippled outline.

Fig. 4.—Side view of alimentary canal and digestive gland.

Fig. 5.—Left side of body, showing distribution of pedal nerves.

Plate XII.—Fig. 6.—Dorsal view of alimentary canal and reproductive system.
Fig. 7.—Dorsal view of alimentary canal and digestive gland.
Fig. 8.—View of right side of reproductive system.
Fig. 9.—Diagram of reproductive system.

Plate XIII.—Fig. 10.—Central nervous system and adjacent nerves.
Fig. 11.—Right side of body, showing distribution of principal nerves.
Fig. 12.—Dorsal view of central nervous system and origin of principal nerves.
Fig. 13.—Lateral view of pericardium, heart and the excretory system with main reservoir, nephrostome, ureter and external opening.



HEATH: CHIORÆRA DALLI.

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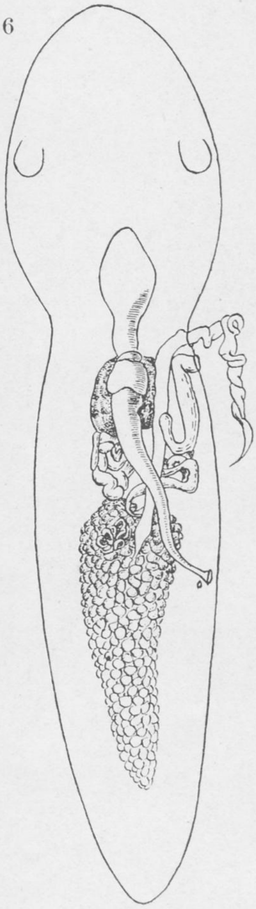

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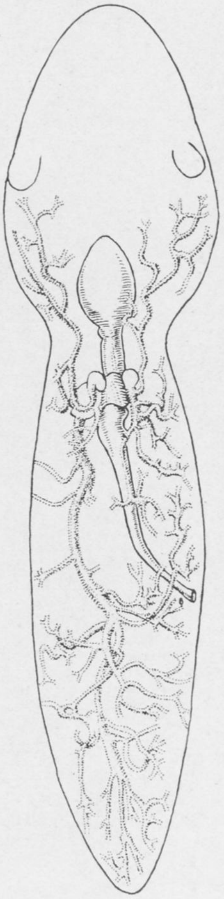

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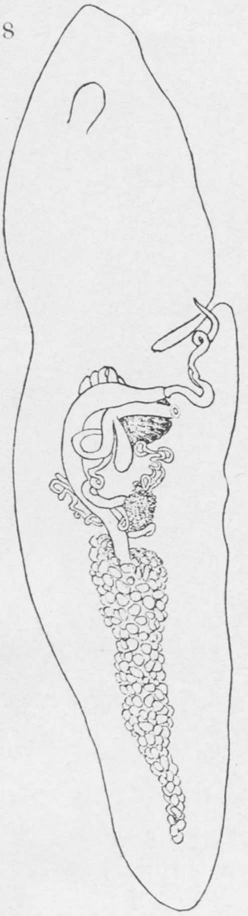

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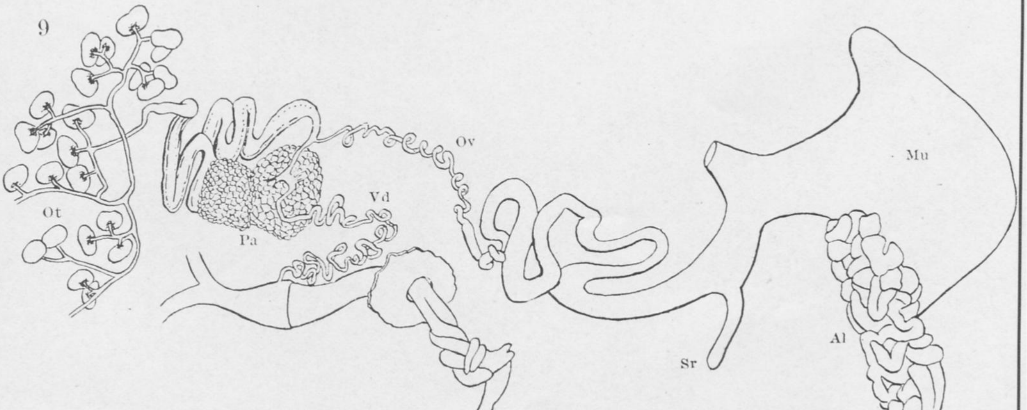

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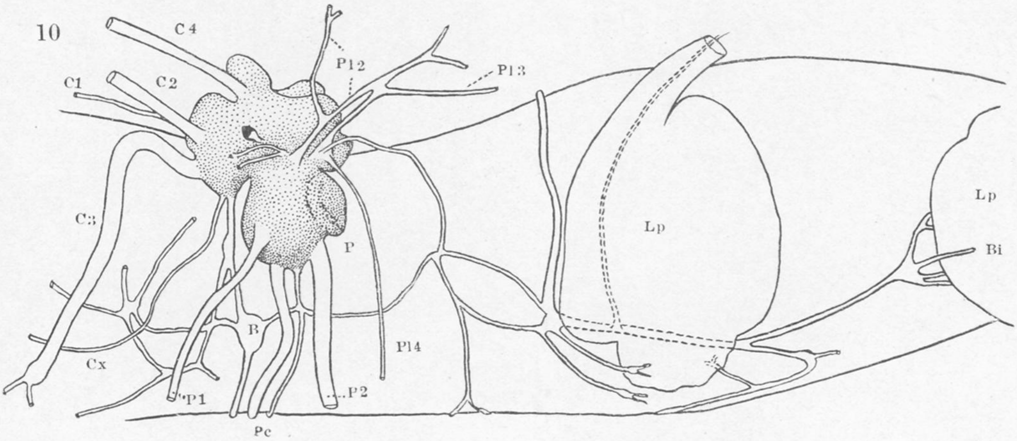

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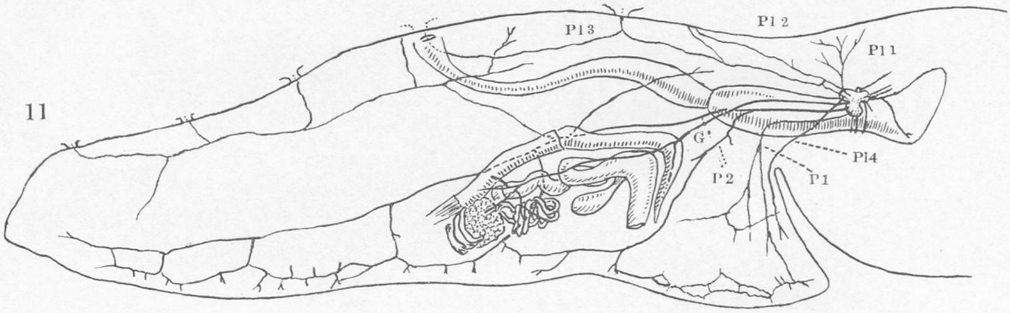

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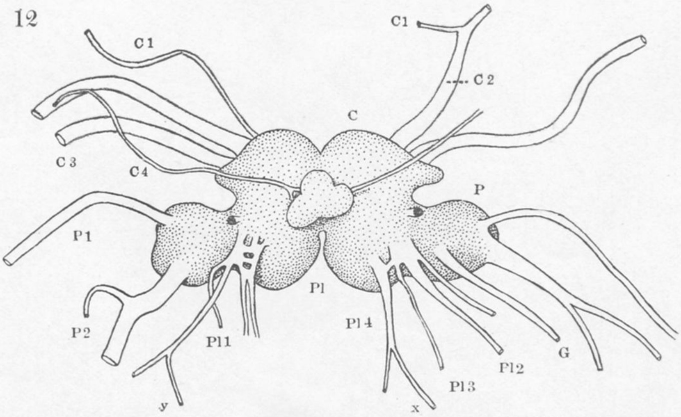

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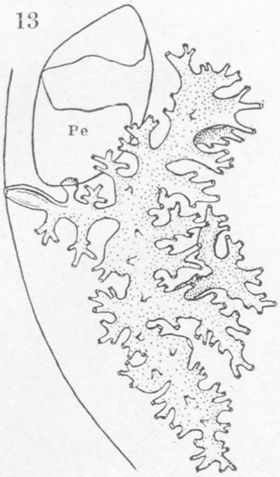

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